ARCTOSTAPHYLOS RAINBOWENSIS, A NEW BURL-FORMING MANZANITA FROM NORTHERN SAN DIEGO COUNTY, CALIFORNIA

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ABSTRACT

Arctostaphylos rainbowensis Keeley & Massihi is a new burl-forming manzanita restricted to northwestern San Diego County and adjacent Riverside County. Previously it had been treated as a disjunct population of the largely Baja Californian *A. peninsularis* P. Wells or a hybrid between *A. glandulosa* Eastw. and *A. glauca* Lindley. Principal components analysis on 48 characters shows that *A. rainbowensis* is distinct from all three of these species. It differs from *A. peninsularis* in its larger leaves with almost twice as many stomata on the abaxial as on the adaxial surface, sparsely glandular puberulent branchlets and rachises, more widely spaced floral bracts, shorter and thicker pedicels, larger fruits that are darker and purple tinged, mealy mesocarp and smooth endocarp. *Arctostaphylos rainbowensis* differs further from *A. peninsularis* in its ecological distribution; *A. peninsularis* is a species of the interior, distributed at elevations above 1200 m whereas *A. rainbowensis* is a low elevation coastal range species. *Arctostaphylos rainbowensis* is distinct from *A. glandulosa* in its diploid chromosome number, non-scabrous leaves, reduced floral bracts, and larger fruits that are round with a solid stone. It differs from *A. glauca* in having a burl, non-reflexed floral bracts, and smaller, non-viscid fruits. *Arctostaphylos rainbowensis* is restricted to approximately 275 km^2 in a region that is undergoing rapid development. In the last 20 years many of the populations have been extirpated, and the species needs legal protection.

RESUMEN

Arctostaphylos rainbowensis Keeley & Massihi, es una especie nueva de "manzanita" que desarrolla nudos, y que está distribuída desde el noroeste del Condado de San Diego hasta los límites del Condado de Riverside, en California. Esta especie ha sido referida como una población disjunta de *A. peninsularis* que ocurre en Baja California, o como un híbrido entre *A. glandulosa* y *A. glauca*. Un análisis componentes principio de 48 carácteres, revelaron que *Arctostaphylos rainbowensis* es distinta a los tres taxa anteriores. Lo se diferencia de *A. peninsularis* porque sus hojas son más grandes, el número de estomas en la superficie abaxial es casi el doble que en la adaxial, raquis y ramificaciones pulverulento-glanduloso, brácteas florales más cortas y separadas, con frutos más grandes y de color púrpura oscuro. Además, *Arctostaphylos rainbowensis* se distingue de *A. peninsularis* en su distribución ecológica, ya que *A. peninsularis* es una especie que se distribuye en montañas por arriba de 1200 m, mientras que *A. rainbowensis* es típica de bajas elevaciones cercanas a la costa. Se distingue de *A. glandulosa* en que es diploide, con un número cromosómico de 13; presenta además hojas no escabrosas, brácteas florales reducidas y frutos grandes, globosos y duros (sólidos). *Arctostaphylos rainbowensis* es separable de *A. glauca* por la presencia de nudos, brácteas florales no reflexas y frutos pequeños, glabros y no viscidos. *Arctostaphylos rainbowensis* esta restringido a una región de aproximadamente 275 km^2 en una región sometida a un rapido desarrollo urbano. Se estima que en el futuro en un periódo de 20 años, una fracción de estas poblaciones serán eliminadas, por lo que estas especies tendrán que tener una protección legal.

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In 1973 a species of *Arctostaphylos* (Ericaceae) new to the California flora was collected by the first author from northern San Diego County. A manuscript naming this new taxon was rejected because one reviewer claimed it was merely a disjunct population of the newly described *A. peninsularis* P. Wells from interior ranges of Baja California (Wells 1972). Subsequently, the San Diego taxon was reported as a range extension of the Baja Californian *A. peninsularis* (Keeley 1974) and others have since listed it in local floras (Beauchamp 1986) and rare plant inventories (Smith and Berg 1988). In the new *Jepson Manual,* however, Wells (1993) omitted it because he no longer believes it is *A. peninsularis,* but now considers it an errant hybrid between *A. glauca* Lindley and *A. glandulosa* Eastw. (Wells personal communication and annotated specimens SD 118009, 118010).

Phenetic analysis reported here demonstrates that the San Diego County taxon is distinct from *A. peninsularis* and is not a hybrid population. This manzanita is described as a new species.

Species Treatment

Arctostaphylos rainbowensis J. Keeley & Massihi, sp. nov. (Fig. 1).—Type: USA, California, San Diego Co., off Rainbow Crest Rd., NE of Rainbow, 3 Aug 1973, *J. E. Keeley 3548* (holotype, LOC; isotypes, CAS, RSA, SD).

Frutices erecti aut arborescentes, 1–4 m alti; caudex tumescens, repullulans post combustum; cortex levis ruber; ramuli glabrati, sparse glandulo-puberuli; folia glauca vel sparse glauca, stomatifera infra duplicato supra, elliptico-ovata, basi rotundatus; petiolo 6–12 mm longo; inflorescentia nascens descendens, paniculata, ramulis 4–10, glabratis, sparse glandulo-puberulis; bracteae subulatae, acuminatae, glabratae, 2–4 mm longae; pedicelli glabri, 3–5 mm longi; corolla alba, urceolata, 6–8 mm longa, 6 mm lata; ovarium glabrum; drupa globosa, glabra, glauca, purpurata, 8–12 mm diametro, mesocarpio crasso, endocarpio solido, nuculis coalescentibus.

Erect shrub or arborescent, 1–4 m high, with large globose burl formed early in development (evident on plants a year old) or large and platform-like on resprouted shrubs. Bark red-brown, smooth. Branchlets seemingly glabrous but microscopically sparsely glandular-puberulent. Leaves seemingly isofacial but with nearly twice as many stomata on lower (abaxial) surface; petioles 6–12 mm; blades 35–50 mm long, 20–35 mm wide, elliptic-ovate, glabrous, moderately glaucous to only slightly glaucous, the margin occasionally serrate, especially on recent resprouts, the base rounded. Panicle descending when immature with well-spaced non-overlapping bracts and exposed buds, 4–10 branches; bracts 2–4 mm, deltoid-subulate,

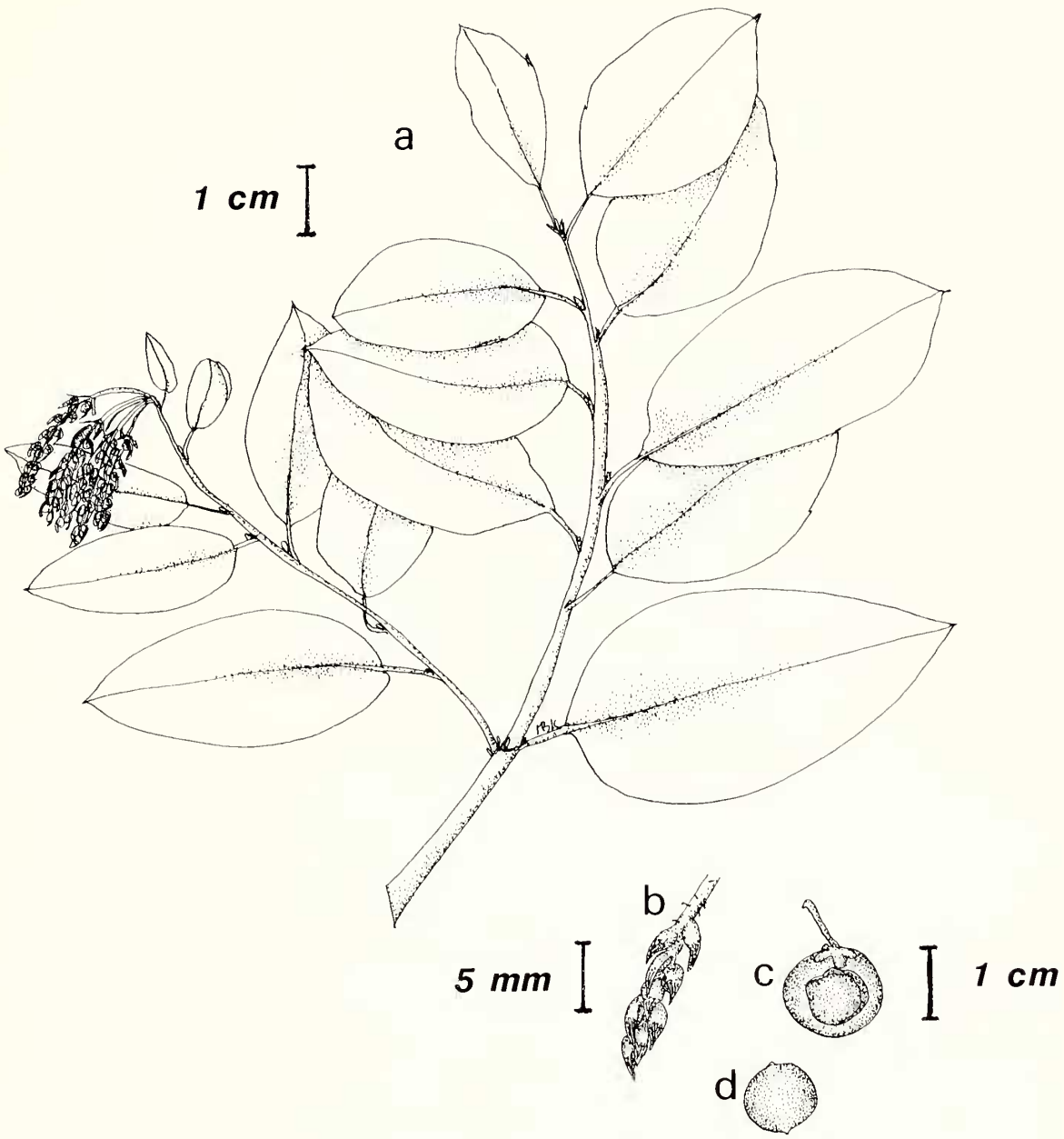

FIG. 1. *Arctostaphylos rainbowensis* (*J. Keeley 3548*). a. Branchlet with nascent inflorescence. b. Single branch of nascent inflorescence. c. Fruit, sepals, and pedicel; mesocarp and endocarp exposed. d. Stone endocarp enclosing multiple seeds (drawing by Melanie Baer Keeley).

keeled, upper-half early marcescent; rachis seemingly glabrous but sparsely covered with short glandular hairs; panicle compact in flower but widely spreading in fruit. Corolla white, urceolate, 5-lobed, pubescent inside, 6–8 mm long; inflated filament bases densely hairy; ovary glabrous. Fruiting pedicel glabrous, thick, 3–5 mm long. Sepals weakly appressed to fruit. Mature fruit globose, 8–12 mm, dark brown with distinct purple tinge and often with whitish bloom, glabrous; mesocarp moderately mealy, dark tan; stone solid, apiculate, without ridges, weakly sculptured. Flowering January–February. $n = 13$ (J. Keeley). The epithet is for the community of Rainbow, near the center of distribution for this species.

Distribution and habit. Arctostaphylos rainbowensis is restricted to northern San Diego County, north of the San Luis Rey River, and southern Riverside County, south of Pauba Valley (Fig. 2), between 300–600 m. It is well represented around the community of Rainbow and east to Mt. Olympus. Its eastern boundary is the Aqua Tibia range and its western boundary is the Santa Margarita Mountains. Total area is approximately 275 km^2. The coastal ranges around Rainbow are dominated by exposed bedrock and very large boulders of acid igneous rock (USDA 1973). Although such sites have been described as of no agricultural value (USDA 1973), in the past two decades many *A. rainbowensis* sites have been replaced by avocado orchards.

Throughout its range *A. rainbowensis* is apparently the sole *Arctostaphylos* species. However, on the edges of its range, in the eastern Santa Margarita Mountains and the western Agua Tibia Mountains, it is sympatric with *A. glandulosa.* These populations usually include individuals that combine traits of both species, suggesting hybridization and introgression between them. *Arctostaphylos glauca* grows in the interior east of *A. rainbowensis. Arctostaphylos peninsularis* is restricted to the interior ranges of northern Baja California and the desert slopes of interior ranges of San Diego and possibly Riverside counties above 1200 m (Keeley unpublished data).

Arctostaphylos rainbowensis is a vigorously resprouting shrub that also produces copious fruits and readily establishes seedlings on disturbed sites created either by wildfires or, more commonly, by bulldozers. On the eastern edge of its range, flowers and fruits are often heavily infested with boring insects.

PARATYPES: USA, California, San Diego Co., Recent burn along unnamed dirt road 6 km N of S–13 off De Luz Rd, 250 m, 29 July 1973, *J. Keeley 3411* (LOC); W face of Mt. Olympus, E of Rainbow, 500 m, 18 Sept 1992, *J. Keeley 21225* (LOC); Pala Rd, 1.5 km S of Rancho Hts Rd, 410 m, 10 Aug 1992, *A. Massihi, R. Goar, J. Keeley 19333* (LOC); Rainbow Hts. Rd, 100 m west of Via Ladera, Rainbow, 400 m, 17 Jan 1993, *Jon E. Keeley 22559* (LOC). Riverside Co., amongst boulders, W of Temecula, 1 km S of Carancho Rd, and W of De Luz Rd, 600 m, 11 Aug 1992, *A. Massihi, R. Goar, J. Keeley 19489* (LOC).

KEY TO THE SOUTHERN CALIFORNIA BURL-FORMING *ARCTOSTAPHYLOS*

The following key, based on studies still in progress, will assist in separating *Arctostaphylos rainbowensis* from other burl-forming manzanitas in southern California. It includes three other taxa not treated in the new *Jepson Manual* (Wells 1993):

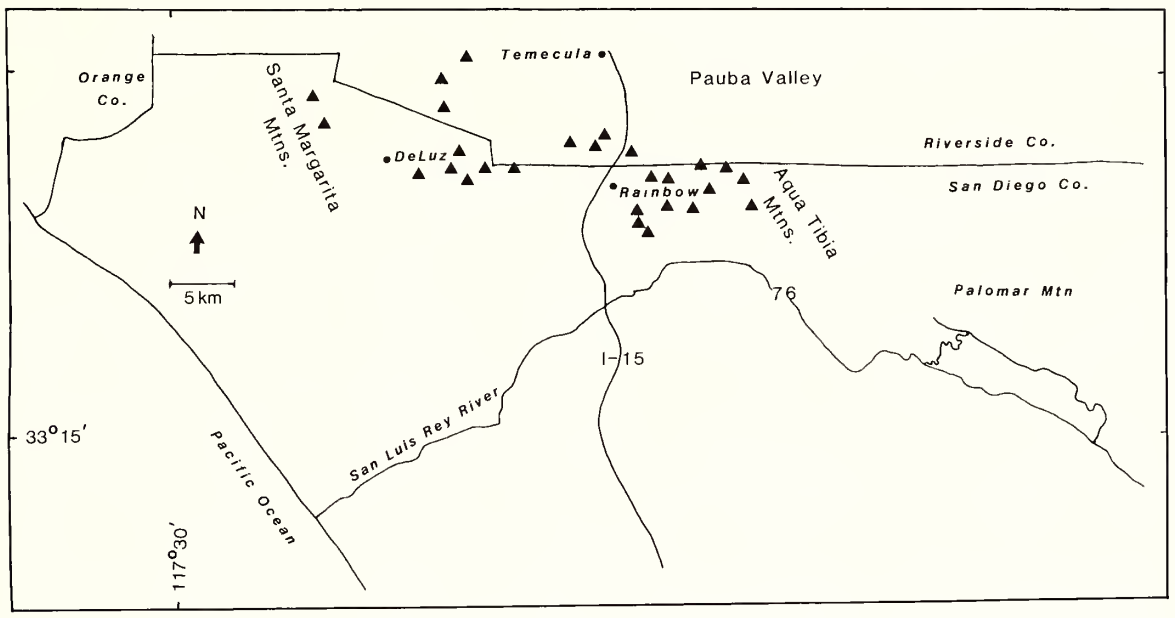

FIG. 2. Distribution of *Arctostaphylos rainbowensis*. Known localities are indicated by triangles.

1. Fruits flattened perpendicular to pedicel (width 1.5–1.7× > length); mesocarp thick and mealy; endocarp separable into 3–5 pyrenes; foliaceous bracts subtending inflorescence 5–15 mm; panicle few branched, compact; (other characters variable); widespread ..... *A. glandulosa*

1′. Fruits globose (width = length); mesocarp thinner, papery, leathery or mealy; endocarp a solid stone; lower bracts highly reduced or absent; panicle few–many branched, spreading

2. Branchlets and rachises tomentose to puberulent; mesocarp leathery

3. Leaves green, not glaucous; fruits 10–12 mm; montane .... *A. parryana* Lemmon (although *A. parryana* is non-burl forming throughout most of its range, there is an undescribed burl-forming *A. parryana* above 1400 m in the San Bernardino and San Gabriel Mtns; it apparently hybridizes with *A. glandulosa* in the latter range and, pending further study, *A. gabrielensis* P. Wells is here treated as such a hybrid).

3′. Leaves glaucous; fruits smaller, 8–10 mm; desert slopes ..... (undescribed taxon with affinities to *A. parryana* and *A. peninsularis,* in the San Jacinto, Santa Rosa, Hot Springs and San Ysidro mtns)

2′. Branchlets and rachises seemingly glabrous and mostly glaucous; mesocarp not leathery

4. Inflorescence bracts not overlapping, tips marcescent; fruits purplish brown; mesocarp mealy; coastal range ..... *A. rainbowensis*

4′. Inflorescence bracts tightly overlapping, not marcescent; fruits orange-red; mesocarp papery; desert slopes ..... *A. peninsularis* (uncommon, NW In-Ko-Pah Mtns, some populations appear to intergrade with *A. glandulosa*)

PHENETIC ANALYSIS OF *A. RAINBOWENSIS* AND OTHER *ARCTOSTAPHYLOS*

Morphometric data were collected from herbarium specimens and used to compare *A. rainbowensis* with the other three species dis-

TABLE 1. CHARACTERS USED IN PRINCIPAL COMPONENTS ANALYSIS AND FACTOR LOADINGS FOR ALL SPECIES (*A. RAINBOWENSIS, A. PENINSULARIS, A. GLAUCA, A. GLANDULOSA*) AND WITHOUT *A. GLANDULOSA*. Percentage of total variance explained was 37% for Factor 1 and 17% for Factor 2 with all four species and 27% for Factor 1 and 19% for Factor 2 with *A. glandulosa* removed.

Character	All four species (Fig. 3)		Without *A. glandulosa* (Fig. 4)	
	Factor 1	Factor 2	Factor 1	Factor 2
Burl	0.30	−0.86	0.89	−0.12
Leaf blade length	0.03	−0.75	0.75	0.26
Leaf blade width	−0.19	−0.45	0.46	0.35
Ratio leaf width/length	−0.28	0.30	−0.31	0.15
Basal angle	0.27	−0.58	0.59	−0.22
Apical angle	0.30	−0.37	0.36	−0.10
Blade shape	0.22	−0.29	0.26	−0.20
Petiole length	−0.25	−0.33	0.31	0.29
Leaf color	0.20	−0.22	0.27	0.28
Leaf glaucousness	0.55	−0.47	0.64	0.20
Leaf scabrousness	0.98	0.08	0.04	0.00
Density of abaxial stomata	0.15	0.43	0.48	0.36
Density of adaxial stomata	0.37	−0.37	−0.39	0.47
Abaxial stomata/adaxial stomata	0.16	−0.76	0.78	0.36
Branchlet pubescence	0.93	−0.26	0.92	0.05
Petiole pubescence	0.97	0.08	0.07	−0.01
Leaf blade pubescence	0.94	0.09	−0.03	0.12
Rachis pubescence	0.93	−0.28	0.92	0.09
Pedicel pubescence	0.82	0.32	−0.49	0.82
Branchlet glandularity	0.94	−0.26	0.94	0.06
Petiole glandularity	0.97	0.06	0.15	0.00
Leaf blade glandularity	0.78	0.06	−0.07	0.05
Rachis glandularity	0.93	−0.25	0.91	0.15
Pedicel glandularity	0.58	0.46	−0.50	0.82
Fruit glandularity	0.09	0.56	−0.52	0.82
Inflorescence length	−0.32	−0.34	0.32	0.09
Number of rachis branches	−0.21	−0.44	0.44	0.00
Bract spacing	−0.69	−0.15	0.17	0.80
Bract keel	−0.88	−0.30	0.64	0.58
Bract shape	−0.06	0.59	−0.12	0.06
Bract marcescence	−0.54	−0.75	0.89	−0.16
Bract reflexed	−0.16	0.44	−0.42	0.76
Bract tip hooked	−0.21	0.51	−0.60	−0.66
Bract length				
Subtending inflorescence	0.84	0.23	−0.32	0.03
Subtending flower bud	0.71	0.12	−0.07	0.58
Pedicel length	−0.05	0.58	−0.60	−0.15
Pedicel width	0.02	−0.74	0.79	0.04
Sepal reflexed	0.59	0.30	−0.34	−0.43
Fruit color	−0.49	0.65	0.74	0.35
Fruit length	−0.66	0.20	−0.28	0.73
Fruit width/fruit length	−0.50	0.31	0.14	−0.00
Fruit weight	−0.47	0.26	−0.25	0.87
Pericarp weight	−0.35	−0.02	−0.02	0.69
Endocarp weight	−0.47	0.33	−0.32	0.84
Mesocarp texture	−0.55	0.74	−0.92	0.16
Endocarp segments	0.91	0.05	0.14	0.01
Endocarp lateral ridges	0.66	0.27	−0.32	−0.70
Endocarp sculpturing	0.55	0.41	−0.49	−0.71

cussed in the introduction. A principal components analysis was plotted to illustrate the interrelationships among all specimens studied.

Species. We collected data from 160 specimens of *A. rainbowensis* from throughout its range (Fig. 2); 70 specimens of *A. peninsularis* from the Sierra San Pedro Mártir and Sierra Juárez of northern Baja California; 30 specimens of *A. glauca* from its range east of *A. rainbowensis* and 30 specimens of *A. glandulosa* from its range south and east of *A. rainbowensis.*

Methods. We used 48 characters in this study; 16 continuous quantitative, 2 meristic, and 27 qualitative characters were recorded and 3 were calculated ratios (Table 1). Qualitative characters were given a ranking from 1 to 5 and each specimen was scored twice by two different persons. For quantitative characters, two samples were measured or weighted for each specimen and the mean was used in the analysis. All character states were standardized by transforming each variable with a z-score obtained by subtracting each observation from the mean of all individuals, and dividing by the standard deviation. This data matrix was used for ordination with principal components analysis using SYSTAT for Windows, Version 5 (Evanston, IL). Characters were compared between populations and species with the Kruskal-Wallis test.

Chromosome counts for *A. rainbowensis* were made from buds collected in January just as they were beginning to enlarge, and preserved in 3:1 ethanol : glacial acetic. Anthers, not yet pigmented, were selected under low power and squashed with aceto-carmine and viewed at 100×. This character was not utilized in the principal components analysis due to the lack of data for *A. peninsularis.*

Stomatal distribution was determined from epidermal peels made of clear nail polish and examined under 40×. All stomata in the field of view were counted and the mean of five different parts of the leaf was used in the analysis.

Results and discussion. The plot of the first two principal components from the analysis of all 290 individual specimens is shown in Figure 3. Ellipses enclose all points for a species and illustrate a clear separation of *Arctostaphylos rainbowensis* from the other three species. Also evident is the overlap in the distribution of *A. peninsularis* and *A. glauca* specimens; all specimens within the zone of overlap with *A. glauca* were the non-burl forming *A. peninsularis* subsp. *juarezensis* J. Keeley, Massihi & Goar.

The loadings of the variables on the first two components indicate the extent to which each character contributes to the variance in this plane (Table 1). Indumentum characters, lower bract length, bract keel and number of endocarp segments contributed most to

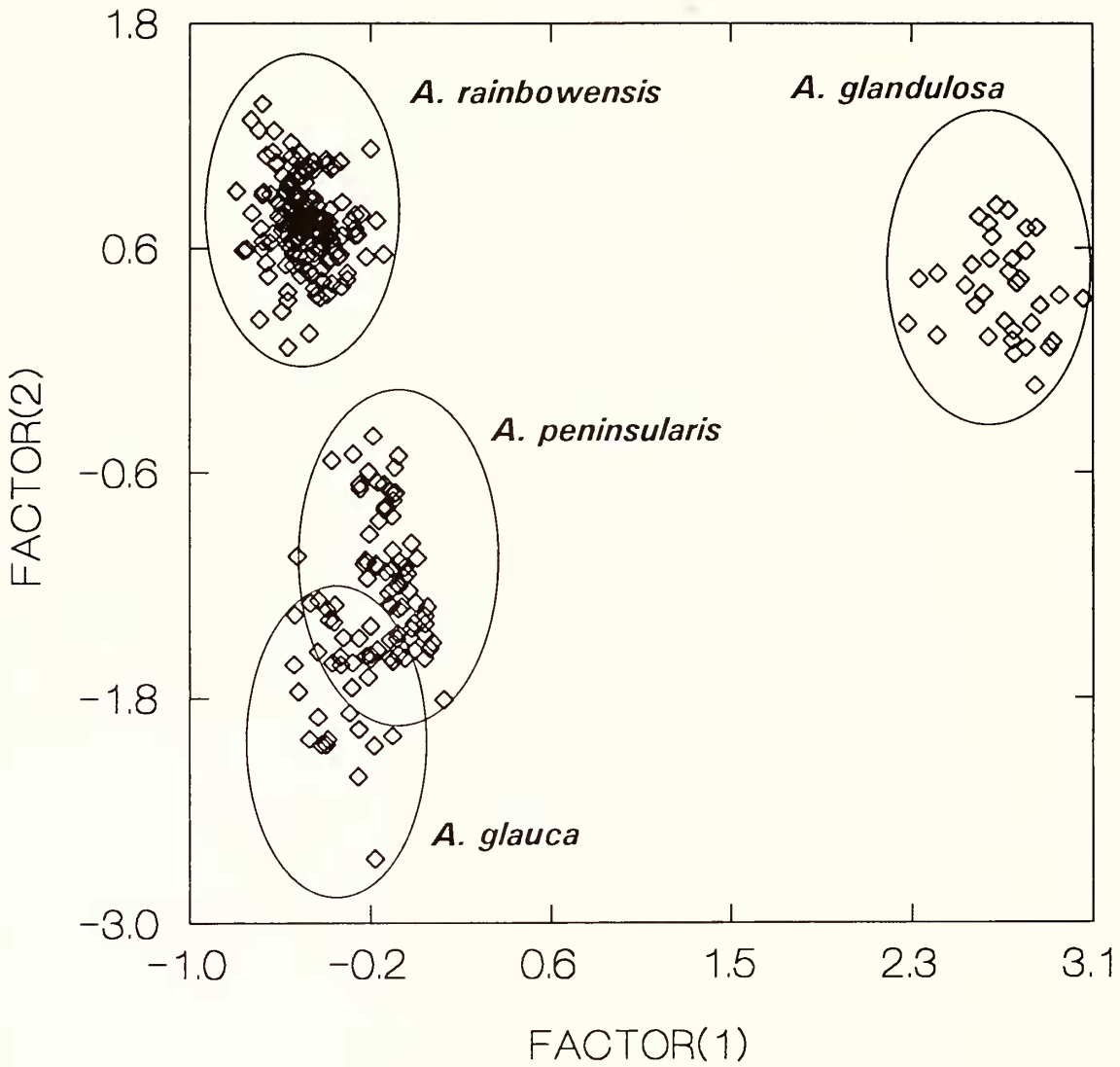

FIG. 3. Plot of principal component analysis using all four species. Relative position of 290 manzanita specimens on the first two principal components of the 48 character correlation matrix. See Table 1 for factor loadings. *Arctostaphylos rainbowensis,* n = 160; *A. peninsularis,* n = 70; *A. glauca,* n = 30; *A. glandulosa,* n = 30.

the separation of *A. glandulosa* from the other three species (Factor 1). Presence of the burl, leaf length, stomatal distribution, bract marcescence, pedicel width, fruit color and mesocarp texture were the important variables separating *Arctostaphylos rainbowensis, A. peninsularis* and *A. glauca* (Factor 2).

These analyses show there is little likelihood of confusing *A. glandulosa* with any of the other three species, however, there is substantial overlap between *A. glauca* and *A. peninsularis.* Therefore, the principal components for these latter two species are plotted along with *A. rainbowensis* in Figure 4. When focusing on these species alone, there is a clear separation of all three, although the total variance explained is only 27% for Factor 1 (Table 1). The component loadings for Factor 1 indicate that the variables most responsible for separating *A. rainbowensis* from the other two species

are: burl, leaf length, branchlet and rachis indument, bract marcescence and mesocarp texture.

In light of the fact that 160 individuals of *A. rainbowensis* are plotted in Figures 3 and 4, it is clear that the range of variation within this species is no greater than that of *A. peninsularis, A. glauca,* or *A. glandulosa.* This pattern is also seen in the comparison of individual characters (Table 2) and is significant in addressing the hypothesis (see introduction) that *A. rainbowensis* is a hybrid population. Hybrid populations, due to recombination and introgression, typically are more variable than true-breeding species. This has been documented in manzanitas at many levels; chemistry (Ellstrand et al. 1987), physiology (Ball et al. 1983), and morphology (Keeley 1976). Based on this pattern, and the fact that *A. rainbowensis* is the only *Arctostaphylos* species throughout most of its range, there is little reason to treat it as a hybrid. However, as may be true for many manzanita taxa, its origin might have involved some ancient hybridization event.

Chromosomal characteristics also reflect on the question of hybridization. Chromosome counts made on plants from four populations throughout the range indicate that *A. rainbowensis* is diploid. For two populations we got reliable counts of $n = 13$. Although precise counts were not possible for the other two populations (because of the way manzanita chromosomes stick together), they were well within the diploid range. The hypothesis that these diploid plants represent hybrids between the tetraploid *A. glandulosa* and the diploid *A. glauca* is not very compelling in light of the fact that chromosomal irregularities were not observed.

Table 2 contrasts the important characters for these four manzanita species. Two of these characters deserve further discussion.

Some burl forming manzanita species are variable for the burl character. For example, *A. peninsularis* subsp. *peninsularis* in the Sierra San Pedro Mártir of Baja California and desert slopes of San Diego County forms burls, whereas *A. peninsularis* subsp. *juarezensis* in the Sierra Juárez of Baja California does not (Keeley et al. 1992). Having collected close to 500 specimens of *A. rainbowensis* from throughout its limited range we have not found any, including young saplings, that lacked burls.

The four species considered in this study differed significantly ($P < 0.01$) in stomatal distribution; stomata are equally distributed on both surfaces in two species and unequally in the other two. This character is relatively constant across the range of *A. rainbowensis* (coefficient of variation for this trait was 21%); stomatal density on the adaxial (top) side was 16–23/mm^2 and on the abaxial side 32–40/mm^2. In contrast, *A. peninsularis* averaged 16/mm^2 and *A. glauca* 32/mm^2 on both surfaces. *Arctostaphylos glandulosa* was similar to *A. rainbowensis* and averaged 26 and 41 stomata/mm^2 on the adaxial

TABLE 2. CHARACTERISTICS OF *ARCTOSTAPHYLOS* SPECIES. Quantitative characters are $\bar{x} \pm SD$; populations with the same superscript letter are not significantly different ($P > 0.05$).

	A. rainbowensis	*A. peninsularis*	*A. glauca*	*A. glandulosa*
Sample size	160	70	30	30
Chromosome #	$n=13$	$n=?$	$n=13$	$n=26$
Burl	Burl	Burl/no burl	No burl	Burl
Leaves				
Length (mm)	41 ± 0.4	29 ± 0.5	33 ± 1.2	37 ± 0.9
Basal angle (°)	$30^{a} \pm 9$	19 ± 11	9 ± 8	$31^{a} \pm 9$
Glaucous	Weakly to intensely	Intensely	Intensely	Weakly to moderately
Scabrous	No	No	No	Yes
Stomatal ratio abaxial/adaxial	1.8 ± 0.4	$1.0^{a} \pm 0.2$	$1.0^{a} \pm 0.1$	1.6 ± 0.3
Branchlet indumentum	Microscopically glandular puberulent	Glabrous	Glabrous	Variously pubescent & glandular
Inflorescence				
Branches (#)	4.1 ± 2.4	$2.2^{a} \pm 1.0$	$2.1^{a,b} \pm 1.0$	$1.8^{b} \pm 0.9$
Bracts				
Spacing	Spaced	Overlapping	Spaced	Overlapping
Marcescent	Strongly	Weakly	Weakly	Not
Length (mm)				
Lower	$1^{a} \pm 2$	$2^{a} \pm 2$	$2^{a} \pm 3$	13 ± 2
Middle	3 ± 1	2 ± 1	4 ± 1	6 ± 2
Sepals reflexed	No	Yes	No	Yes
Fruits				
Color	Purplish-brown	Orange-red	Brown	Orange-red
Length (mm)	9.5 ± 1.5	8.9 ± 1.2	13.6 ± 1.3	5.6 ± 1.3
Ratio width/length	$1.1^{a} \pm 0.6$	$1.0^{a} \pm 0.1$	$1.0^{a} \pm 0.1$	1.7 ± 0.3
Pericarp	Mealy-leathery	Papery	Papery	Very mealy
Endocarp				
Segments	Solid stone	Solid stone	Solid stone	3–5 pyrenes
Surface	Smooth	Ridges & sculpturing	Smooth	Ridges & sculpturing

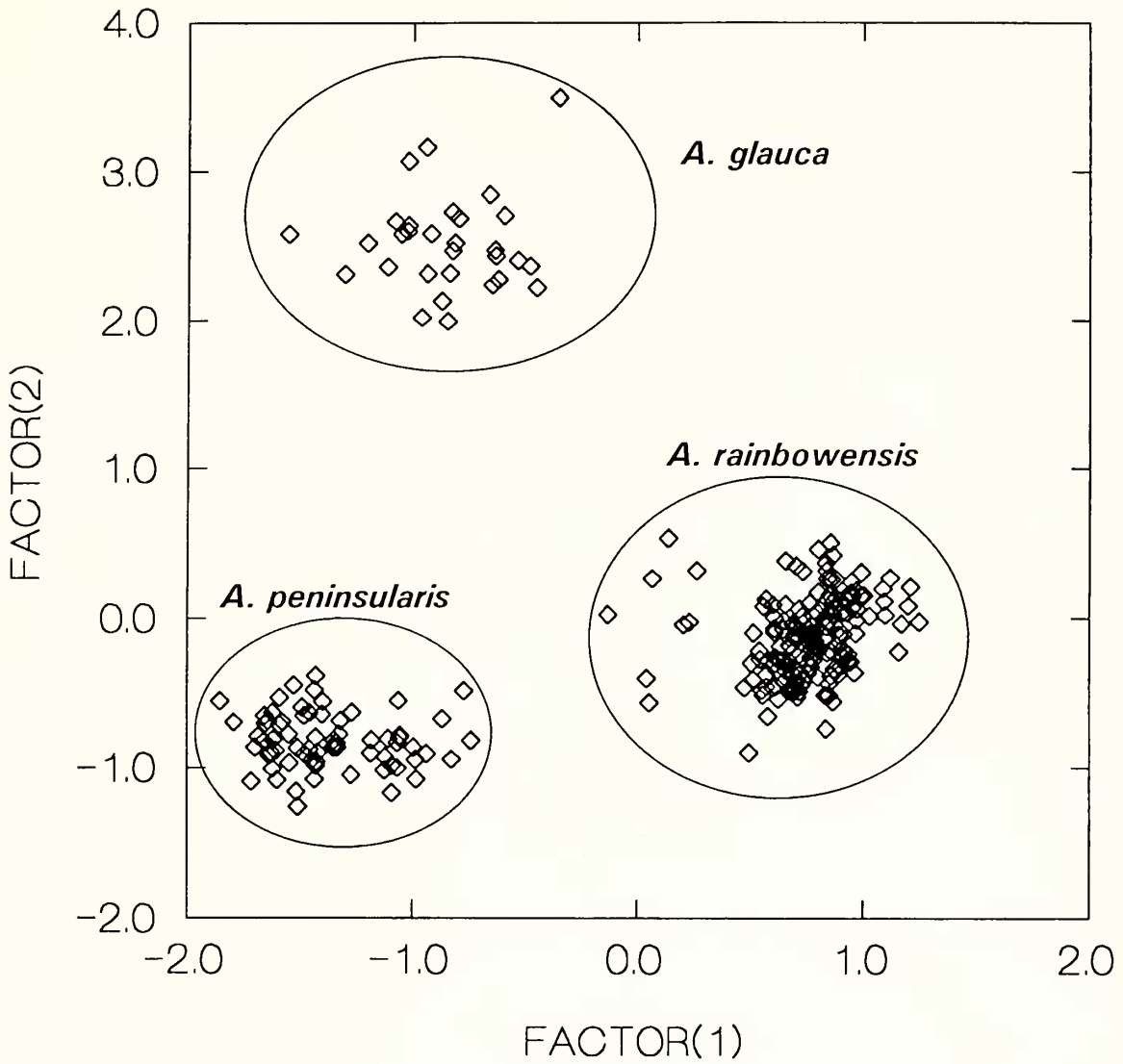

FIG. 4. Plot of principal component analysis without *A. glandulosa*. Relative position of 260 manzanita specimens on the first two principal components of the 48 character correlation matrix. See Table 1 for factor loadings. *Arctostaphylos rainbowensis*, n = 160; *A. peninsularis*, n = 70; *A. glauca*, n = 30.

and abaxial surfaces, respectively. This agrees with the report by Howell (1945); however, Knight (1981) and Wells (1987) reported equal number of stomata on the two surfaces for *A. glandulosa*. The patterns we found support the conclusions of Howell (1945) that unequal distribution of stomata is typical of coastal manzanitas, whereas equal distribution is typical of interior species. While stomatal distribution probably is not a highly reliable phylogenetic marker, it does suggest quite different ecophysiological modes between coastal taxa such as *A. rainbowensis* and interior ones, such as *A. peninsularis*.

Based on many traits such as reduced scale-like bracts and fruits with solid stones, *A. rainbowensis* is clearly aligned with both *A. peninsularis* and *A. glauca*, and this is reflected in their alignment in Figure 3. It seems likely that these three species share a close

ancestry. Sorting out the exact phylogeny may prove to be a challenge as the high incidence of suspected hybridization in the genus (Ellstrand et al. 1987) leads to predictions of highly reticulate patterns of evolution. Certainly the manner in which these three species combine traits (Table 2) is consistent with such a model of evolution for the genus.

Acknowledgments

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